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Title: Bottlenose dolphins retain individual vocal labels in multi-level alliances

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Summary

Cooperation between allied individuals and groups is ubiquitous in human societies, and vocal communication is known to play a key role in facilitating such complex human behaviours [1,2]. In fact, complex communication may be a feature of the kind of social cognition required for the formation of social alliances, facilitating both partner choice and the execution of coordinated behaviours [3]. As such, a compelling avenue for investigation is what role flexible communication systems play in the formation and maintenance of cooperative partnerships in other alliance-forming animals. Male bottlenose dolphins in some populations form complex multi-level alliances, where individuals cooperate in the pursuit and defence of an important resource, access to females [4]. These strong relationships can last for decades and are critical to each male's reproductive success [4]. Convergent vocal accommodation is used to signal social proximity to a partner or social group in many taxa [5,6], and it has long been thought that allied male dolphins also converge onto a shared signal to broadcast alliance identity [5–8]. Here, we combine a decade of data on social interactions with dyadic relatedness estimates to show that male dolphins that form multi-level alliances in an open social network retain individual vocal labels that are distinct from those of their allies. Our results differ from earlier reports of signature whistle convergence among males that form stable alliance pairs. Instead, they suggest that individual vocal labels play a central role in the maintenance of differentiated relationships within complex nested alliances.

Keywords: vocal labels, alliances, cooperation, bottlenose dolphin, male social relationships, signature whistles, vocal learning

Results and Discussion

Animals that form strong social bonds tend to vocally accommodate one another by converging onto shared calls [5,6]. Convergent vocal accommodation is used to signal social proximity to a partner or social group [5,6,9] and has been well documented in a variety of birds and non-human mammals, such as chickadees [10], parrots [11], bats [12], primates [13,14] and elephants [15]. Phonetic convergence in humans has also been linked to relationship strength, where stronger bonds lead to a higher degree of convergence [16]. Further, convergence onto shared or similar identity signals has been documented in allied male bottlenose dolphins (both *Tursiops aduncus* and *T. truncatus*) [7,8].

Bottlenose dolphins are adept vocal production learners, a notably rare skill in mammals [17], and use vocal learning to develop their individually specific signature whistle, which they use to broadcast their identity [18]. Signature whistles are developed within the first few months of an individual's life and are structurally unique from conspecifics [17,19]. The pervasive notion that alliance partners will converge onto a shared signature [6–8] is perhaps surprising, given that the signature whistle is a rare example of a non-human mammal using a learned vocal label that can be considered somewhat comparable to a human name [20]. However, suggested benefits of 'alliance signatures' include broadcasting alliance identity as a specific social unit towards other allied males or to sexually receptive females [6,8]. Whilst one study showed that allied males tend to have signature whistles that are more similar to their partner's than to non-partners [7], this finding was based purely on dyadic relationships. In Shark Bay, Western Australia, males cooperate together in pairs or trios, known as first-order alliances, to sequester and control the movements of single oestrous females [4]. Each male, in turn, belongs to a second-order alliance of 4–14 males, considered the core unit of male social organisation, who work together to acquire and defend females [4]. Whistle convergence was previously documented amongst males in Shark Bay, but the study was limited to one trio in an unusual recording context and did not

consider partnerships outside this first-order alliance [8]. Thus, the influence of nested alliance relationships on whistle similarity between cooperative partners remains unknown. Here, we investigated signature whistle convergence in first- and second-order alliances in Shark Bay, Western Australia, where our long-term dolphin research project has been conducted on a seasonal basis since 1982. We collected focal follow data on allied males and used acoustic localisation and the SIGID (SIGnature IDentification) method [21] to identify individual signature whistles. We also used long-term photo-identification records to determine the strength of alliance associations (calculated over a 10-year period) and single nucleotide polymorphisms (SNPs) to estimate dyadic relatedness between males. These analyses were carried out in order to determine whether strong social bonds and/or genetic relatedness influence whistle similarity between cooperative partners.

Signature whistle similarity between alliance partners

We identified the signature whistles of 17 individual adult males that comprise six first-order alliances across three different second-order alliances (Table 1, Figure 1, see Figure S1 for determination of alliance membership). The majority of signature whistles were confirmed using acoustic localisation, with the exception of two whistles that were confirmed by exclusion (see *Methods*), where the whistles of all other alliance partners were known (Table 1). Whistle similarity between allied and non-allied males was quantified using two methods: visual classification by human judges [7,20] and a dynamic time warp analysis [22]. The 12 human judges (blind to context and identity) showed substantial inter-observer agreement in their signature whistle similarity scores (mean weighted kappa statistic: 0.7, $P < 0.0001$).

Visual classification

We found no evidence of whistle convergence, with mixed–effect models detecting no effect of social relationship strength and/or genetic relatedness on whistle similarity (Figure 2A, Data S1).

Furthermore, similarity scores of ≥ 3, which indicate higher levels of similarity, were more common between males in different second-order alliances than within alliances (Figure 2B). Thus, allied males tended to have signature whistles that were less similar to their alliance partners, with only one male (MOG) found to have the highest similarity score solely with a first-order partner (Figure 2).

Dynamic time warp analysis

The dynamic time warp approach allowed us to expand from a single model signature whistle per male to a set of 10 signature whistles per male. Pairwise dissimilarities were relatively consistent across whistle replicates, with few exceptions (Figure S2). Similar to the visual classification analysis, mixed-effect models detected no effect of social relationship strength and/or genetic relatedness on dynamic time warp whistle similarity (Figure 3A, Data S2). Allied males did not have signature whistles that were more similar to their alliance partners. In fact, the mean similarity for first- and second-order alliance partners was no different from the mean similarity between males from different second-order alliances (Figure 3B). The most similar signature whistle was found predominantly (13 of 17 cases) in males from different second-order alliances, and, again, in only one case did an individual have the most similar signature whistle with his first-order alliance partner (Figure 3C).

Conclusions

We detected no evidence of signature whistle convergence between cooperative partners in nested bottlenose dolphin (*T. aduncus*) alliances. Our results differ from prior research, which suggested that closely affiliated male dolphins produce similar signature whistles [7,8]. We also found no evidence of genetic relatedness influencing signature whistle similarity between males. Most of the males in this study had signature whistles that were notably different from those of both first- and second-order alliance partners. Our findings, therefore, suggest that individual

vocal labels, rather than shared identity calls, play a central role in maintaining recognition within complex nested alliances.

The lack of a genetic influence on whistle similarity between males is unsurprising, given that signature whistle development is strongly influenced by vocal learning [17]. The fact that many of the allied males in our study have signature whistles with low similarity scores is likely a result of differences in their early acoustic and social environments. Of the seven dyads in our study that were first sighted together when still dependent calves, none had a visual whistle similarity score greater than 2 (mean =1.6). There is some evidence to suggest that calves develop signature whistles that resemble those of relatively rare associates of their mothers [19]. Therefore, male calves of mothers with strong associations would be expected to develop whistles with low similarity. Furthermore, the nine dyads in our study that had relatively high visual whistle similarity scores (≥ 3) were first sighted together as sub-adults (mean = 9.5, range: 3-15), i.e. when their signature whistles were already developed. The majority of their individual sightings histories pre-date their first joint sighting. Although one of those dyads consisted of first-order alliance partners, this is no more than expected by chance, with our broader results demonstrating a striking lack of convergence.

Our findings differ from the original study on whistle convergence that was conducted on three male dolphins within the Shark Bay population [8]. These males formed an alliance over a four-year period and appeared to have converged onto one shared whistle type [8]. However, their alliance formed under abnormal conditions where the recordings were obtained, i.e., in shallow water by a beach where humans regularly provisioned them with fish. The small sample size and unusual context may explain their findings. While our research clearly demonstrates the lack of long-term vocal convergence in signature whistles between adult male dolphins in Shark Bay, it provides only a snapshot of existing alliances over the duration of the study. For example, we

were unable to determine whether these signature whistles had been modified during the lifetime of each male. However, at least one adult male (COO) in an established alliance uses the same signature whistle first recorded when he was an infant (1.5 years of age) over a quarter of a century ago [23], supporting the notion that signature stability in males can span decades, as it can in females [24].

Interestingly, allied pairs of common bottlenose dolphins (*T. truncatus*) in Sarasota Bay, Florida, do tend to have signature whistles that are similar in structure [7]. Selection may favour the convergence of such calls within a dyad if there is only one partner to vocally accommodate. In that instance, convergence between individuals within a pair may function in signalling their commitment to one another, as shown for avian duetting [25]. However, in a society in which nested alliances are formed, where males within second-order alliances show notable differences in partner preferences [4] and where first-order alliance stability can vary [4], there may be no adaptive benefit to signature whistle convergence. Instead, there appears to be a strong benefit in retaining an individual signature whistle that is distinct from one's allies.

Vocal accommodation in humans has been suggested as serving as a phenotypic "tag" for cooperation, where the convergence of dialects facilitates cooperation between individuals [5,26,27]. The lack of a relationship between social proximity and vocal similarity in our study would suggest that such tags are not required for cooperation. However, it should be noted that, while human children can acquire new dialects, accommodation in adults involves only subtle shifts and rarely leads to completely new dialect acquisition [5]. As such, speech accommodation during short dyadic interactions can promote social identity between individuals [5,16], but there is no evidence of long-term convergence of identity signals in humans. In fact, the ability of individuals to have control over with whom they cooperate plays an important role in stabilising large-scale cooperation in human societies [28]. The structure of social networks can promote

choosiness and a need to monitor the behaviour of others to optimise partner choice [29]. This places a demand on the recognition of a large number of individuals and their third-party relationships with other conspecifics [30]. Thus, in those species that form nested alliances, individual vocal labels may reliably facilitate the recognition of many cooperative partners and competitors in complex biological markets [31]. Indeed, the bottlenose dolphin's propensity for the use of learned vocal labels [20] and long-term social recognition [32] may well have enabled the formation of their nested alliances.

In contrast to our study system, many non-human animals converge on group distinctive identity calls as a means of promoting group cohesion and strengthening social bonds [6]. So, under what evolutionary conditions is the convergence of identity calls favored? The study of animal populations with similar phylogenetic traits to those of the Shark Bay dolphins, such as fission-fusion social systems, vocal flexibility, and long-term social memory, may shed light on this important question. For example, under certain conditions, it appears that the importance of individual vocal labels in forming and maintaining cooperative strategies may well take precedence over any conferred benefits of vocal convergence. If that is the case, then other affiliative strategies are required to indicate social proximity.

The two obvious mechanisms for mediating social proximity between male dolphins in Shark Bay are affiliative tactile contact and synchrony [33]. Males mediate alliance relationships with gentle contact behaviours, such as petting, as a means of maintaining their strong male-male bonds, similar to primate grooming [30,33,34]. In chimpanzees, grooming between partners with strong social bonds has been directly linked to oxytocin release [35], and the role of oxytocin in facilitating bonding between humans and other animals has been well documented [36,37]. Increased oxytocin release has also been linked to social synchrony in humans [38], promoting trust [37], cooperation [36] and social bonding [39]. Synchronous behaviour may, therefore,

have evolved as a coalition signalling system in human societies to indicate the quality of the cooperative relationship [40]. We know that synchrony also plays an important role in affiliative interactions between male dolphins in Shark Bay [30]. In fact, it is synchrony, rather than shared identity calls, that functions as a signal of unity [30,33], representing convergence with humans in the use of synchrony to promote both cooperation and coordination between allied males [36]. Thus, nested alliances in dolphins appear to be similar to those in humans; in which synchrony is an adaptive signal indicating quality of relationship [33,40], but recognition is maintained through individual vocal labels or ‘names’.

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Author contributions

SLK conceived the study, acquired funding, collected data, conducted the analysis and drafted the manuscript; MK, RCC, SJA, and WF acquired funding; WF, SJA, LG, SW, RCC, MK significantly contributed to data collection; MK, LG, SW conducted the genetic analysis; FJ conducted the dynamic time warping analysis; all authors edited the manuscript, provided critical review and gave final approval for submission.

"The authors declare no competing interests."

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Main Figure Legends

Figure 1. Social network of 17 adult males grouped in their second-order alliances; only CoAs ≥ 0.2 are shown as this reliably identifies second-order alliance partners, and males are colour-coded by alliance membership. The thickness of the lines indicates the strength of the dyadic social relationship, and alongside each male is a spectrogram of his signature whistle (sampling rate: 96kHz, FFT length: 1024, Hanning window function). See also Figure S1 for determination of alliance membership.

Figure 2. Analysis of whistle similarity based on visual classification: (A) network plots of the three second-order alliances where males are colour-coded by alliance membership; the left network shows pairwise relationships between males with Coefficients of Association ≥ 0.2, and the right network plot shows the pairwise median similarity scores that are ≥ 3 from the visual classification; (B) non-linear multidimensional scaling of the pairwise whistle similarity scores. See also Data S1 and Table S1.

Figure 3: Analysis of whistle similarity based on dynamic time warping: (A) non-linear multidimensional scaling of pairwise dissimilarity values; (B) mean whistle similarity (dissimilarity values were log-transformed and then standardized to z-scores for each individual before pooling) according to alliance membership. Note that the categories are exclusive so that pairs in the second-order alliance category are not from the same first-order alliance; (C) number of individuals where the male with the most similar signature whistle was a first- or second-order alliance partner or in a different alliance. Colours represent first-order alliance membership. See also Data S2, Figure S2 and Table S2.

Main Tables

Table 1. Summary of the 17 adult males used in this study, their second-order alliance membership, mean association coefficient (CoA) for their first-order alliance, their age in years and the number of signature whistles recorded for each male across days and years. All males have significant home range overlap [4] and frequently interact with one another. See also Figure S1.

Second-order alliance ID code	*First-order alliance mean CoA*	*Individual male ID code*	*Age (years)*	*# Signature whistles recorded (days/years)*
KS	0.7	PON	est. > 30	34 (8/3)
		QUA*	29	20 (3/2)
		PAS	32	64 (6/4)
	0.5‡,	CEB	31	35 (11/4)
		MOG	est. > 30	26 (3/2)
		DEE	31	30 (5/3)
		IMP	est. > 30	24 (8/3)
	0.33	NOG*†	est. > 30	22 (1/1)
		DNG	32	31 (3/3)
PD	0.76	RID	est. > 30	60 (7/3)
		FRE	est. > 30	32 (7/5)
		BIG	est. > 30	12 (3/2)
	0.88	NAT	est. > 30	36 (6/4)
		WAB†	est. > 30	24 (3/3)
RR	0.65	COO	29	40 (6/3)
		SMO	29	36 (4/2)
		URC	27	36 (5/3)

* QUA not seen in 2017; NOG not seen after 2013

† Signature whistles confirmed by exclusion, where all other signature whistles within the first-order alliance had been localised to other individual males (*Methods*).

‡, Only three of these males consort together at any one time, but consorting partners changed frequently among the four.

STAR Methods

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Stephanie King (stephanie.king@uwa.edu.au).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We worked with free-ranging adult male bottlenose dolphins (*Tursiops aduncus*) in the eastern gulf of Shark Bay, Western Australia, where our long-term dolphin research project has been running on a seasonal basis (typically austral winter and spring) since 1982. Males ranged from approximately 27 to 40 years old.

METHOD DETAILS

Acoustic data collection

Acoustic data were collected during focal behavioural follows of allied male dolphins between August and September 2016 and June to September 2017. Focal follows were conducted from a 5.4 m research vessel using a towed hydrophone array consisting of four HTI-96 MIN series (flat frequency response: 0.002–30 kHz +/- 1 dB) in a similar configuration to Quick et al. [41]. Recordings were made onto a TASCAM DR-680 MKII multi-track recorder at a sampling rate of 96 kHz. A spoken track was used to note the bearing (compass bearing, where the boat's bow is 0°), distance (m) and identification of the focal animals at each surfacing. Aerial video was also used to document animal movement and relative position, with the use of a GoPro Hero4 attached to a 1 m^3 Allsopp Skyshot Helikite, which was attached to the bow of the boat using flying line and an Okuma Solterra Game Fishing Reel and flown at an altitude of c. 30 m. The

522 aerial video allowed us to simultaneously record the movements, including some subsurface
523 movements, of multiple individuals over much larger distances than visual observations from the
524 research vessel allowed. The aerial video data also assisted in the interpretation of the acoustic
525 localisation.

526 Individual dolphins were identified by trained observers on the research vessel via their
527 unique dorsal fins, and corroborated with photo-identification data collected using a Canon 50D
528 camera and 100-400 mm IS lens. Group composition was verified every five mins and all
529 changes in group composition were recorded *ad lib* during focal follows; these data were
530 synchronised to recordings prior to analysis. The engine was switched off during recordings and
531 only whistles with a good signal to noise ratios were used for localisation. Localisation error of
532 the array was calculated using custom-written MATLAB routines to calculate 2D averaged
533 MINNA (minimum number of receiver array) localisations using the methods described in
534 Wahlberg et al. [42] and Schulz et al. [43]. The array was calibrated using two different
535 frequency modulated dolphin whistles, each approximately 1.5 seconds in duration with a
536 frequency range of 4-20kHz. Acoustic localisation errors for directions (n = 75) were calculated
537 as 76% within ± 15 degrees, and 99% within ± 30 degrees.

538 Additional acoustic data were collected during focal follows of allied males between
539 August and November 2013 and September and November 2014, using a single towed
540 hydrophone designed by the Scripps Whale Acoustics Lab at the University of California, San
541 Diego. The hydrophone was equipped with a low-frequency transducer (flat frequency response:
542 0.4–15 kHz +/- 3 dB) and a high-frequency transducer (flat frequency response: 15 kHz–120
543 kHz +/- 8 dB) with a notch at 25 kHz, which were summed before digitising. Recordings were
544 made onto a Fostex FR-2 memory recorder at a sampling rate of 192 kHz. Animal identity and
545 group composition data collection followed the methods described above. These single
546 hydrophone data assisted in characterising the whistle repertoire of our focal alliances.
547

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550 ***Behavioural data collection: Strength of male relationships***

551 Survey data were used to calculate association indices between pairs of males. A "survey" is a
552 minimum five-min observation of dolphin group composition ("group" being defined by the 10-
553 m 'chain rule') and behavioural activity [44]. Survey data are collected annually as part of our
554 long-term research program, with behavioural survey data spanning 35 years. For this study,
555 pairwise Coefficients of Association (CoA) were calculated over a 10-year period using
556 SOCPROG 2.7 [45] and the Simple Ratio Index (SRI). The SRI is an estimate of the proportion
557 of time two animals spend together (0 for pairs of animals that never associate; 1 for pairs
558 always seen together) [46,47]. CoAs were calculated using the last 10 years of survey data for
559 each male prior to it last being seen alive (two males disappeared during our study). The
560 sampling period was day and only association data recorded in the first five mins of a survey
561 were used. Restriction to the use of just the first five minutes of observation ensured that
562 association measures were comparable across all surveys.

563

564 To confirm that a CoA cut-off value of 0.2 reliably identified second-order alliance partners, we
565 conducted a changepoint analysis using the Pruned Exact Linear Time (PELT) method
566 (*changepoint package* in R) on the SRI coefficients of 66 adult males in eastern Shark Bay. Only
567 CoA values greater than zero were used in the analysis. The first changepoint occurred at a SRI
568 coefficient of 0.2, a cut-off value that is in line with previous studies [4,44]. We therefore used ≥
569 0.2 as a cut-off for second-order allies, and first-order allies were based on hierarchical
570 clustering with coefficients ranging from 0.33 to 0.88 (Figure S1). All allied males in this study
571 were also frequently observed consorting females together, thus alliances were defined not only
572 by their association indices, but also their functional behaviour. All social network figures were
573 plotted in SOCPROG 2.7 [45] and Gephi 0.9.2 [48].

574

575 ***Signature Whistle Identification***

576 Initially, spectrograms (fast Fourier transform (FFT) length 1024, Blackman-Harris window)
577 were inspected in Adobe Audition CC v. 2017.0.2 (Adobe Systems) for instances of signature
578 whistle production. Signature whistles are highly stereotyped and often produced in repetitive
579 sequences [21]. Frequency contours were then extracted from each whistle spectrogram (1024
580 FFT, overlap 87.5%, Hanning window, time resolution of 1.333 ms) in MATLAB using a
581 supervised contour extraction program [49], with a time resolution of 10 ms. Contour files were
582 then categorised according to their frequency modulation pattern using an automated adaptive
583 resonance theory neural network that incorporates dynamic time warping; ARTwarp [49].
584 ARTwarp categorises contours based on a set degree of similarity, also known as the vigilance
585 parameter, which, in this instance, was set to 91, as per previous studies [50]. This approach
586 allowed individual signature whistle types to be objectively grouped together in the same
587 category [49], and the ARTwarp analysis was conducted separately for each focal follow.

588

589 Each whistle type category was then confirmed as a signature whistle using the SIGID method
590 [21], which uses the temporal patterning that is unique to signature whistles to identify them in
591 free-ranging animals. Whistles were confirmed as signature whistles if the ARTwarp category
592 had at least four whistles in it, and at least once in the sequential bout analysis, 75% or more of
593 those whistles occurred within 1–10 seconds of one other whistle in that same category [21].
594 Additionally, each signature whistle also had to be either (1) localised to an individual male that
595 was > ± 30° from any other individual at least once to confirm identity, and/or (2) confirmed by
596 exclusion where all other signature whistles within the first-order alliance had been localised to
597 an individual male.

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602 ***Acoustic Similarity***

603 *Visual Classification*

604 Visual classification was used to determine signature whistle similarity between allied males, as
605 per previous studies [7,20,51,52]. A signature whistle template from each male was chosen at
606 random, and all whistle templates were plotted as spectrograms with standardised time and
607 frequency axes (scales not plotted). A total of 12 human judges (blind to context and animal
608 identity) were individually asked to rate the similarity of pairs of signature whistles (190
609 combinations in total), using a five-point similarity index ranging from 1 (least similar) to 5
610 (most similar) [7,20,51,52]. Template whistles did not change configuration between judges, but
611 the order of slide presentation was randomized in order to eliminate presentation bias. A
612 weighted Cohen's kappa statistic was used to quantify agreement between pairs of judges, which
613 accounts for the degree of disagreement between the judge's ordinal scores [53]. Median
614 similarity scores are provided in Table S1.

615

616 *Dynamic Time Warp Analysis*

617 Additionally to visual classification, a dynamic time warp approach [22] was used to quantify
618 more subtle differences in whistle similarities based on the shape of the fundamental frequency
619 contour [54]. Ten signature whistle templates were chosen for each male. Signature whistles
620 often include multiple repetitions of nearly identical loops [55], and the focus of this analysis
621 was to quantify fine-scale similarity between individual signature whistle loops. The
622 fundamental frequency contour was extracted in MATLAB by calculating a spectrogram (24 Hz
623 spectral resolution, 10 ms temporal resolution, 50% overlap, 40 dB dynamic range), and then
624 using a manually supervised ridge tracker to detect and store local peaks in the spectrogram.
625 Gaps were inserted manually between loop repetitions to facilitate isolating individual loops

during analysis. To calculate a dissimilarity score, the fundamental frequency contour of each loop was isolated, and the mean fundamental frequency subtracted to account for frequency generalization [56]. A non-Euclidean dynamic time warp distance was calculated using a standard, dynamic time warp algorithm that allowed for unrestricted temporal extension or compression at each time point. To compare whistles with a different number of loops, we calculated an average dissimilarity metric for each pair of whistles by taking the mean dynamic time warp distance across all possible combinations with a single loop from each whistle. Finally, we calculated the dissimilarity between each pair of bottlenose dolphin males as the mean dynamic time warp (DTW) distance across all 10 signature whistles (Table S2).

Dyadic Genetic Relatedness

Genetic data were obtained from small tissue biopsy samples, which were previously collected as part of our long-term research program using a remote biopsy system [57]. Dyadic genetic relatedness between all males in this study was calculated using polymorphic single nucleotide polymorphisms (SNPs) generated by a double digest restriction site associated DNA sequencing (ddRAD) approach [58]. Quality filtered reads were aligned against a *T. truncatus* reference assembly obtained from the NCBI RefSeq database (GenBank accession GCA_001922835.1 [59]). Alignment against the reference assembly was done using *bowtie2* version 2.2.6 with the 'very-sensitive' preset. A 'variant-only' vcf file was produced using *HaplotypeCaller* from the Genome Analysis Toolkit GATK version 3.7-0 [60,61], resulting in 302,012 raw variant calls. Based on call quality (phred quality score >30), sequencing depth (each locus sequenced at least five times), missing individuals (> 70% individuals covered), and minimal distance between each SNP of at least 100kb, we identified 3,396 high-quality biallelic SNPs per individual [62]. We then used the software Coancestry V1.0.1.5 [63] to estimate pairwise relatedness between individuals using the triadic maximum likelihood estimator [64] (Table S3).

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical procedures were conducted in R 3.3.2 (R project for statistical computing; GNU project). To determine whether or not allied males tended to have signature whistles more similar to each other we conducted two different analyses. First, we ran a cumulative link mixed model (clmm using *ordinal* package in R) on the pairwise median similarity scores as determined by the human judges. Model predictors were pairwise COAs (calculated over a 10 year period) and pairwise relatedness (using polymorphic SNPs). To control for repeated measures of individuals, individual IDs were included as random effects. The full model was compared to nested models, and a null model containing only the random effects. Model selection was performed by ranking them using Bayesian Information Criterion (BIC), log-likelihood (logLik), and Akaike's Information Criterion (AIC), where the model with the best fit had the lowest aforementioned criterion values. However, models within two AIC units can be considered comparable (Data S1). We also employed anova using the *car* package in R to test whether the inclusion of different parameters in the model explained significantly more variance (Data S1). Second, we ran a linear mixed-effect model fit by REML (lmer using *lme4* package in R) on the mean pairwise dissimilarity scores calculated from the DTW distance. Dissimilarity scores were log transformed (log10) to better fit with an additive variance model. Model predictors and model selection were all as per the analysis conducted on the human judge scores (Data S2). R^2 values for linear mixed-effect models were calculated using the *r.squaredGLMM* function (*MuMIn* package in R) [65]. Finally, to check for correlation between the two signature whistle dissimilarity matrices, we conducted a Mantel test (mantel using *vegan* package in R). The pairwise median similarity scores, as determined by the human judges, were first converted to dissimilarity scores (D) where D = 1-(similarity score-1)/4. The mantel statistic was based on Pearson's product-moment correlation and was calculated using 10,000 permutations [66]. There was significant correlation between the dissimilarity matrices produced by the two different

analytical techniques (Mantel test $r = 0.38$, $P = < 0.0001$), revealing some agreement between the two approaches.

KEY RESOURCES TABLE

Data S1. Cumulative link mixed model predicting median similarity scores between each pair of male bottlenose dolphins as a function of social association (CoA) and dyadic genetic relatedness. (A) Model selection for the cumulative link mixed model results for the human judge median similarity scores. Failure to reject the null model using Bayesian Information Criterion (BIC), log-likelihood (logLik), Akaike's Information Criterion (AIC), Δ AIC, and ANOVA (Pr(>Chisq)). **(B)** To determine the importance of the random effect we compared the full model to a fixed effects only model using *anova.* **(C)** Parameter estimates for the full model. Confidence intervals for both parameters intersect zero, indicating there is little evidence that either parameter affects whistle similarity. **Related to Figure 2.**

Data S2. Linear mixed-effect model predicting log transformed dynamic time warp dissimilarity scores between each pair of male bottlenose dolphins as a function of social association (CoA) and dyadic genetic relatedness. (A) Model selection for the linear mixed-effect model results for the log transformed DTW dissimilarity scores. Failure to reject the null model using Bayesian Information Criterion (BIC), log-likelihood (logLik), Akaike's Information Criterion (AIC), Δ AIC, and ANOVA (Pr(>Chisq)). R^2 for mixed-effect models calculated using the *r.squaredGLMM* function (*MuMIn* package in R); where *marginal* R^2 describes proportion of variance explained by fixed effects alone, and *conditional* R^2 describes the proportion of variance explained by both fixed and random effects [S1]. **(B)** Parameter estimates for the full model. Confidence intervals for both parameters intersect zero, indicating there is little evidence that either parameter affects whistle similarity. **Related to Figure 3.**